

The Defective Color Vision in Juvenile Goldfish Does Not Depend on Used Training Task as the Measure of Discrimination: A Two-choice Response Measure

KEN OHNISHI

*Department of Physiology, Nara Medical University,
Kashihara, Nara 634, Japan*

ABSTRACT—Color discrimination ability of juvenile goldfish (*Carassius auratus*) was measured using a Y-maze training technique to test whether the defective color vision in juveniles found in a previous study [10] would be similarly observed using another training paradigm. The discrimination ability of juveniles was compared with that of adults that had been previously obtained with the same training paradigm [9]. Although the juveniles trained with green and red discriminative stimuli (colored papers) showed good discrimination ability comparable to that of the adults, the juveniles had great difficulty in discriminating blue from both green and red while the adults did not. These results are in agreement with findings in the previous study [10] using a “go/no-go” task. The defective color vision of juveniles is clearly not task-dependent but is rather a general property originating from the developmental process of blue vision.

INTRODUCTION

A previous study [10] on the development of color vision in goldfish has clearly shown that juveniles have defective color vision, specifically for color blue, when it is examined with a “go/no-go” training technique. It may be possible, however, that they can process blue information normally and discriminate blue from other colors as do adults when they are confronted with another training paradigm. The neural pathway (especially the blue information processing pathway) in juveniles that produces avoidance responses might not yet have developed fully compared with other neural pathways subserving other types of behavior. It is still unclear whether or not the defective color vision observed in the previous study [10] is task-specific. Many behavioral studies on spectral sensitivity indicate that the property of any spectral sensitivity depends on the training task. For example, the reflex-like startle response tends to be triggered predominantly by long-wavelengths [2, 13]. A more complex behavior,

such as a two-choice discriminative response, is produced by short- and mid-wavelengths as well as long-wavelengths [6, 15, 16]. Yager [15] reported that short-wavelengths are most effective for the two-choice type of response. It seems that a definite spectral region is dominantly processed in a neural pathway when a certain type of behavioral pattern is used as the measure of a discriminative response.

In addition to such task-dependency, the color vision of goldfish also depends on the intensity levels of background illumination and discriminative lights. The vision for red is defective under low levels of background illumination when the fish are trained on a “dark” test field [7, 8]. The color vision disappears in wavelength discrimination performed at a low intensity of discriminative lights when trained on an “illuminated” test field [8]. In this condition, the fish use a “brightness” cue but not a “color” one. Considering the lighting-condition dependence of color vision as well, in this study, the discriminative colored papers were presented under a relatively high intensity level of background illumination (about 1000 lx) compared with that in the previous study (15 lx; [10]).

MATERIALS AND METHODS

The same size juvenile goldfish (3–5 cm, age of <1 year) as those used in the previous study [10] were trained to discriminate between three types of paired colored papers, blue vs. green, red vs. blue and red vs. green, using the same Y-maze instrumental conditioning technique employed and described in detail in another former study [9]. In brief, juvenile fish were rewarded with food when they chose a correct stimulus in such a way that they swam into one of the choice chambers. For brightness control, the colored papers which had been adjusted to be of equal subjective brightness were adopted in this study as well. The maxima of reflectance (λ_{\max}) of the colored papers was 480 nm in blue, 520 nm in green and 660–700 nm in red. In the two cases of blue/green and blue/red discriminations in juveniles, the blue papers of higher brightness (about 5% higher in relative brightness than for adults) were used, taking into account the juveniles' lower blue sensitivity [10].

RESULTS

Juveniles, unlike adults, showed very poor abilities in color discrimination between blue and green and red and blue as shown in Figure 1 and 2a. In particular, in the discrimination between blue and green, the percentages of correct responses for the juveniles ($n=11$) were very low and not incremental (they did not increase over 60% in later sessions), whereas those for the adults ($n=6$) reached about 90% by later sessions: all data on the adults' color discrimination used in this study were taken from a previous study [9]. Significant differences between the correct responses were observed in the two groups (for statistical analysis, a three-way analysis of variance was used: Groups, $F(1, 15)=52.18$, $P<0.01$; Days, $F(7, 105)=8.33$, $P<0.01$; Groups \times Days, $F(7, 105)=3.90$, $P<0.01$). Similarly, in the discrimination of blue/red, those for juveniles ($n=23$) were not as high as for adults ($n=6$; Groups, $F(1, 27)=8.80$, $P<0.01$; Days, $F(7, 189)=24.42$, $P<0.01$; Groups \times Days, $F(7, 189)=0.93$, $P>0.05$). Some juveniles ($n=10$), however, showed adult-like color discrimination ability (Fig. 2b). No significant differences

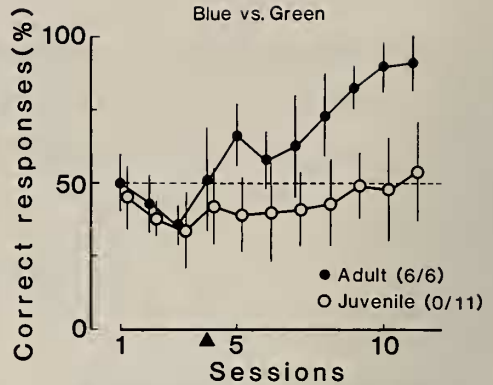


FIG. 1. Learning curves in juveniles (\circ , $n=11$) and adults (\bullet , $n=6$) trained with the blue vs. green stimuli. The fish were rewarded only when they responded to a correct stimulus (a stimulus less frequently responded to during the pretraining trials) during the training trials. The filled triangle indicates the start of the training trials. The numbers in the parentheses indicate learners/trained fish. Vertical bars, \pm SD.

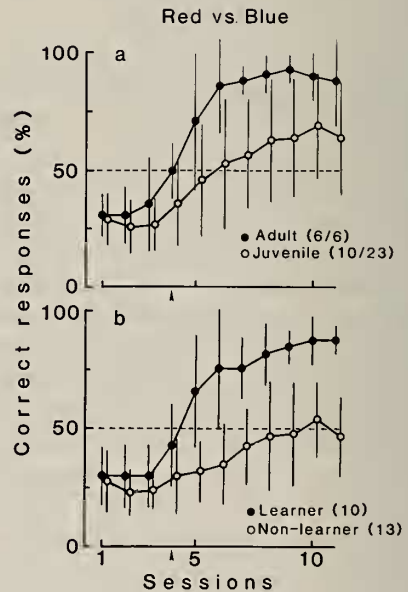


FIG. 2. Learning curves in juveniles (\circ , $n=23$) and adults (\bullet , $n=6$) trained with the red vs. blue stimuli (a) and those in learners (\bullet , $n=10$) and non-learners (\circ , $n=13$) of the juveniles (b). Significant differences were observed in (a) but the juvenile learners showed a very similar learning curve to that of adults as shown in (b). See Figure 1 for further explanations.

were observed between the correct responses of the juvenile learners (the fish which showed over 75% correct responses for at least 3 days successively: all trained adults fulfilled this criterion) and adults (Groups, $F(1, 14)=1.65$, $P>0.05$; Days, $F(7, 98)=24.54$, $P<0.01$; Groups \times Days, $F(7, 98)=0.30$, $P>0.05$). The percentages of correct responses of non-learners ($n=13$) in this task of discrimination were very low (Fig. 2b); they did not increase over 50% in later sessions like those of juveniles in the discrimination between blue and green. Contrarily, in the discrimination between red and green (Fig. 3), the juveniles ($n=12$) showed a good, adult-like color discrimination ability. Their correct responses were not significantly different from those of adults ($n=7$; Groups, $F(1, 17)=1.61$, $P>0.05$; Days, $F(7, 119)=9.37$, $P<0.01$; Groups \times Days, $F(7, 119)=0.50$, $P>0.05$). When the juveniles had acquired the learned responses, the tasks of discriminating between the reinforced colored papers and gray papers with various brightnesses were performed to make sure that the fish did not discriminate among the colored papers on the basis of brightness. The fish correctly discriminated the reinforced colored papers from the gray ones, showing similar percentages of correct responses to those for color discrimination. Thus, the juveniles clearly used a color cue, but not a brightness cue, in the color discriminations.

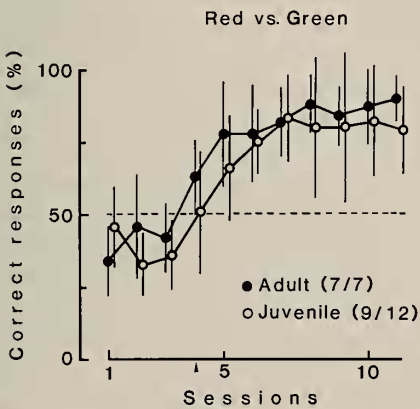


Fig. 3. Learning curves in juveniles (\circ $n=12$) and adults (\bullet , $n=7$) trained with the red vs. green stimuli. No significant differences were observed between the curves. See Figure 1 for further explanations.

To test whether another type of visual discrimination ability is normal in juveniles, brightness discrimination was performed using white and black papers. Figure 4 shows that juveniles ($n=12$) could normally discriminate differences in brightness. Their correct responses clearly increased with the increment of training sessions as did those of adults (about 80% correct responses in later sessions) and were not significantly different from those of adults ($n=6$; Groups, $F(1, 16)=0.33$, $P>0.05$; Days, $F(7, 112)=20.29$, $P<0.01$; Groups \times Days, $F(7, 112)=1.16$, $P>0.05$). This indicates that brightness discrimination ability is normal in juveniles.

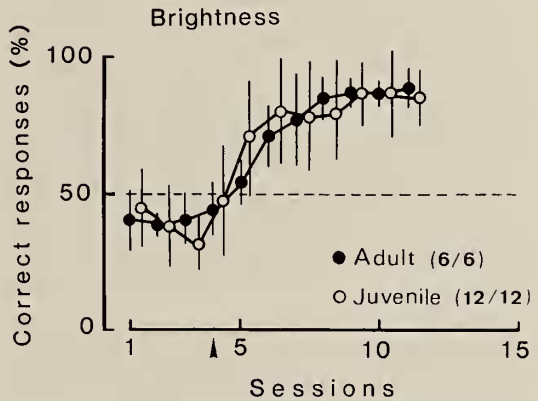


Fig. 4. Brightness discrimination in juveniles (\circ , $n=12$) and in adults (\bullet , $n=6$). All trained juveniles showed adult-like clear learned responses. See Figure 1 for further explanations.

TABLE 1. Percentages of learners in the 3 types of color discrimination measured with 2 training techniques

	blue vs. green	red vs. blue	red vs. green
Two-choice			
Juveniles	0 (0/11)	43 (10/23)	75 (9/12)
Adults	100 (6/ 6)	100 (6/ 6)	100 (7/ 7)
Go/No-go*			
Juveniles	0 (0/10)	0 (0/ 9)	70 (7/10)
Adults	33 (4/12)	50 (6/12)	70 (7/10)

The numbers in the parentheses indicate learners/trained fish. *The data (10 training periods) are from [10].

The percentages of learners in this study, together with those measured in the previous study [10], are shown in Table 1. No juveniles trained to discriminate between blue and green could fulfill the criterion defining "learner" (0%), but some juveniles (43%) showed clear learned responses in the discrimination between red and blue. In the discrimination between red and green, many more juveniles (75%) could acquire the learned responses. The brightness discrimination was easy for all trained juveniles to learn (100%). All trained adults fulfilled the criterion defining "learner" in the three types of color discrimination as well as the brightness discrimination.

DISCUSSION

There are several important differences in the training methods used in this study and those of the previous one [10]. The correct responses of the fish were reinforced with a reward (food) and motivated by appetite in this study while they were reinforced with punishment (electro-shock) and motivated by fear in the previous study. The discriminative stimuli were presented simultaneously using colored papers under a 1000 lx background illumination in this study, while they were presented successively using monochromatic lights under a 15 lx background illumination in the previous study. It has been reported that the intensity level of background illumination considerably affects the color vision of goldfish. The tetrachromatic color vision becomes trichromatic and, furthermore, the spectral sensitivity function becomes the luminosity function with the decrease in its intensity [7, 8]. Moreover, the fish seem to use a brightness cue at a low intensity (detectable level) of discriminative lights but they use a color cue for high intensity (about 1.0 log unit higher than the detectable level) of discriminative lights for wavelength discrimination when they are trained on an "illuminated" test field [8]. The evidence led to the assumption that the previously observed defective color vision in juvenile goldfish [10] may be due to the low intensity of background illumination. Such a possibility, however, can be rejected because this study, which was performed under a high intensity (about 1000 lx) of background illu-

mination, also demonstrated defective color vision. Thus, the defect in color vision of juveniles is thought to originate from the developmental process of the neural system of blue vision.

Another aspect of interest in this study is that some juveniles showed an adult-like discrimination ability in the discrimination between red and blue but none for the discrimination between blue and green (Table 1: The training task of the present study was probably more easy for the fish to acquire discriminative responses than that of the previous study [10]. The numbers of adult learners in the present study were relatively large compared with those in the previous study [10].). This difference in the discrimination ability between blue vs. green and red vs. blue may be due to the different quantal absorption ratio of the mid-wavelengths to the long-wavelengths sensitive cones among "blue", "green" and "red" spectral regions. The quantal absorption ratio of the mid-wavelengths to the long-wavelengths sensitive cones in "blue" spectral region is more similar to that in "green" spectral region than that in "red" spectral region [1]. In "blue" and "green" spectral regions, the quantal absorption of the long-wavelengths sensitive cones is not ignorable. Contrary to this, in "red" spectral region, the quantal absorption of the mid-wavelengths sensitive cones seems to be insignificant. Thus, the discrimination between blue and green is probably more difficult than that between red and blue for juveniles who may have not the functionally matured short-wavelengths sensitive cones (The quantal absorption of the ultraviolet sensitive cones is insignificant in visible spectra [1].). Although this explanation is based on the immaturity of the receptor level, the possible immaturity of the post-receptor level should keep in mind. If the short-wavelengths sensitive cones have matured, some juveniles may have already developed a matured blue/red opponent processing pathway but not yet a blue/green one at the same stage of growth.

It is unknown, at present, whether the poor blue vision of juveniles originates from receptor or post-receptor elements. However, as already discussed before [10], some possible explanations of the poor blue vision of juveniles can be propo-

sed, considering the morphological studies on the development of the retinal neurons [3–5, 11, 12, 14]. Those neurons of goldfish are very unique in such a respect that they continue to grow and further are added newly beyond larval stages into adult life, while in most vertebrates this neurogenesis is completed during early postembryonic stages. Such unique neurogenesis may have a relation to the prolonged development of blue vision.

REFERENCES

- 1 Bowmaker JK, Thorpe A, Douglas RH (1991) Ultraviolet-sensitive cones in the goldfish. *Vision Res* 31: 349–352
- 2 Cronly-Dillon JR, Muntz WRA (1965) The spectral sensitivity of the goldfish and the clawed toad tadpole under photopic conditions. *J Exp Biol* 42: 481–493
- 3 Johns PR (1981) Growth of fish retinas. *Amer Zool* 21: 447–458
- 4 Johns PR, Easter SS (1977) Growth of the adult goldfish eyes. *J Comp Neurol* 176: 331–342
- 5 Meyer RL (1978) Evidence from thymidine labeling for continuing growth of retina and tectum in juvenile goldfish. *Exp Neurol* 59: 99–111
- 6 Neumeyer C (1984) On spectral sensitivity in the goldfish: evidence for neural interactions between different “cone mechanisms”. *Vision Res* 24: 1223–1231
- 7 Neumeyer C, Arnold K (1989) Tetrachromatic color vision in the goldfish becomes trichromatic under white adaptation light of moderate intensity. *Vision Res* 29: 1719–1727
- 8 Neumeyer C, Wietsma JJ, Spekrijse H (1991) Separate processing of “color” and “brightness” in goldfish. *Vision Res* 31: 537–549
- 9 Ohnishi K (1991) Goldfish’s visual information processing patterns in food-reinforced discrimination learning between compound visual stimuli. *J Comp Physiol* 168: 581–589
- 10 Ohnishi K (1993) Development of color vision in goldfish: selective delayed maturation of blue vision. *Vision Res* 33: 1665–1672
- 11 Peng YW, Lam DMK (1991) Organization and development of horizontal cells in the goldfish retina, I: The use of monoclonal antibody AT101. *Visual Neurosci* 6: 357–370
- 12 Peng YW, Lam DMK (1992) Organization and development of horizontal cells in the goldfish retina, II: Use of monoclonal antibody MH1. *Visual Neurosci* 8: 231–241
- 13 Powers MK (1978) Light-adapted spectral sensitivity of the goldfish: a reflex measure. *Vision Res* 18: 1131–1136
- 14 Raymond PA (1990) Horizontal cell axon terminals in growing goldfish. *Exp Eye Res* 51: 675–683
- 15 Yager D (1967) Behavioral measures and theoretical analysis of spectral sensitivity and spectral saturation in the goldfish *Carassius auratus*. *Vision Res* 7: 707–727
- 16 Yager D (1969) Behavioral measures of spectral sensitivity in goldfish following chromatic adaptation. *Vision Res* 9: 179–186